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Thermoregulation by rhesus monkeys at different absolute humidities

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Abstract The effect of relative humidity on thermoregulation has been well examined. Because the same relative humidity represents very different absolute humidities at different ambient temperatures, the present study was designed to examine the interaction of temperature and absolute humidity on the thermal balance of rhesus monkeys, *Macaca mulatta*. Thermal balance was examined in six unacclimated, unanesthetized, female rhesus monkeys at ambient temperatures of 25, 30, 35, and 40 °C and absolute humidities of 6, 22, and 40 torr. Monkeys were capable of achieving thermal balance under all conditions except at 40 °C with 40 torr absolute humidity, where experiments were stopped after rectal temperature exceeded 40.5 °C. At 40 °C, monkeys increased evaporative heat loss through both respiration and sweating; the slope of the relationship between evaporative heat loss and core temperature was attenuated by increases in absolute humidity. In contrast, absolute humidity had no direct effect on metabolic rate. The rise in body temperature under the conditions of high heat/high humidity was therefore most attributable to humidity-dependent decreases in evaporative heat loss.

Keywords Thermal balance · Metabolic rate · Temperature

Abbreviations E_{tot} : total evaporative heat loss · HR : heart rate · K : thermal conductance · M : metabolic

rate · RQ : respiratory quotient · T_c : core temperature · T_{sk} : mean skin temperature · $V\text{CO}_2$: carbon dioxide production · $\dot{V}\text{O}_2$: oxygen consumption

Introduction

The effect of humidity on thermoregulation by mammals has long been appreciated, particularly at high ambient temperatures (Candas et al. 1982; Gagge and Gonzalez 1996; Pandolf et al. 1974; Reece et al. 1972; Shvartz and Benor 1972). Thermoregulation in hot, humid environments is less effective due to the compromise of evaporative cooling; evaporative cooling potentially decreases with increasing humidity, resulting in an increase in body temperature (Gagge and Gonzalez 1996). Interestingly, humidity has also been suggested to affect thermoregulation at temperatures below the thermoneutral zone (Burton and Edholm 1955; Iampietro et al. 1958; Iampietro and Buskirk 1960). To date, no clear physiological explanation has emerged to explain the enhanced perception of cold in a “wet, cold” environment.

Most studies investigating the effect of humidity on thermoregulation have used different relative humidities as experimental treatments, rather than absolute humidities (e.g., Cochrane and Sleivert 1999; Iampietro and Buskirk 1960; Klemm and Hall 1972; Shapiro et al. 1980). This may be sufficient when comparing thermoregulatory responses at a single temperature, where relative and absolute humidities will be directly related. Using this approach, for example, Garby et al. (1986) demonstrated that increases in absolute humidity (resulting from differences in unregulated atmospheric relative humidity) in humans at a single ambient temperature (24 °C) did not alter sensible heat loss but did decrease evaporative heat loss. For different ambient temperatures, however, the same relative humidity will represent very different absolute humidities; because of this, systematic investigations of the effects of absolute

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humidity at different ambient temperatures requires a fairly sophisticated environmental chamber, as has been pointed out previously (Kenney and Zeman 2002). Recently, Kenney and Zeman (2002) have used such a chamber to determine critical environmental limits for lightly exercising humans over fairly narrow ranges of temperature (34–38 °C) and absolute humidity (12–20 torr).

To our knowledge, the more basic determination of how absolute humidity affects thermoregulation at various ambient temperatures in resting mammals has not been performed. For example, although elegant thermal balance studies have been performed in monkeys (Johnson and Elizondo 1979; Kolka and Elizondo 1983), complementary studies of absolute humidity effects on this thermal balance have not been done. We therefore sought to characterize any effects of absolute humidity on thermoregulation by determining the thermal balance in the rhesus monkey, *Macaca mulatta*, over a wide range of ambient temperatures (20–40 °C) and absolute humidities (6–40 torr).

Materials and methods

Animals

Unacclimated female rhesus monkeys (*Macaca mulatta*, six 4-year-old juveniles, 3.98 ± 0.55 kg) were housed individually in standard stainless-steel monkey cages in a windowless room at 24 ± 2 °C with a 12L:12D light cycle. Because they were juveniles, the monkeys did not yet menstruate. Monkeys were provided a diet of monkey chow (Purina) supplemented with fresh fruit twice daily. Water was available ad libitum.

Thermal balance

Each monkey was trained to sit quietly in a Plexiglas primate-restraining chair by placing it in the chair for 2–4 h/day for 10 days. Following this training period, each animal was placed in a similar restraint chair in a hypobaric chamber [810 cm (wide) \times 810 cm (height) \times 760 cm (depth)] equipped with ambient temperature and humidity controls. Both temperature and humidity were servo-controlled at any preset experimental value. Dry- and wet-bulb thermometers were placed within the chamber.

Physiological measurements were collected from monkeys randomly assigned to ten temperature/humidity combinations; experiments on any given monkey were separated by at least 1 week. Animals were exposed to ambient temperatures of 25, 30, 35 and 40 °C at absolute humidities of 6, 22, and (at 35 and 40 °C) 40 torr. Monkeys were allowed to sit quietly for a 1-h equilibration period in the specified environment, with measurements taken at the end of this 1-h period. In

order to ensure the safety of the monkeys, however, experiments at 40 °C and 40 torr were discontinued if core temperature (T_c) rose above 40.5 °C, and measurements were made at this point. Dry- and wet-bulb temperatures within the environmental chamber were recorded.

At each temperature/humidity regime, core and skin temperatures, heart rate (HR), oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$), evaporative water loss, and internal thermal conductance (K) were determined. T_c was measured by a thermistor (YSI Model # 701) inserted approximately 8 cm into the rectum. Mean skin temperature (T_{sk}) was estimated using the equation of Kolka and Elizondo (1983) and skin temperature measurements taken from the left chest, upper back (interscapular), base of the tail, upper thigh, and calf regions using surface thermistors (YSI Model # 709X) attached with contact cement.

HR was measured by electrocardiography using surface electrodes attached to the right chest and both lower legs. The electrocardiogram was monitored with a Hewlett Packard Defibrillator (Model 43100A), the output of which was used to trigger a cardiometer.

$\dot{V}O_2$ and $\dot{V}CO_2$ were determined from the airflow (4–6 l/min) drawn through a 2.5-l head chamber and the respective fractional concentration differences of O_2 and CO_2 of gas entering and exiting the head chamber. Airflow was measured by a Kurz 565-7A Mass Flowmeter. O_2 and CO_2 concentrations were determined by a Perkin-Elmer 11000 Medical Gas Analyzer. Instruments were calibrated prior to each experiment and checked upon completion of each experiment using custom-mixed test gases that bracketed the physiological range of values observed during pilot experiments. Metabolic rate (M) was estimated from $\dot{V}O_2$, CO_2 production and respiratory quotient (RQ) according to Johnson and Elizondo (1979).

Respiratory evaporative water loss was measured as the absolute humidity difference between air entering and leaving the head chamber, multiplied by the airflow. Respective absolute humidities were determined by the temperature differential between wet- and dry-bulb thermometers positioned in the air stream both before and downstream from the head compartment. Total evaporative water loss was estimated as the change in body mass, measured by an electronic balance to the nearest 0.01 kg, during each climatic exposure. Urine or feces lost during the climatic exposure period were collected in a tared pan containing a layer of mineral oil, then weighed to account for body mass loss other than evaporation. Evaporative heat loss was determined as the product of the total evaporative water loss and the latent heat of vaporization of water.

K was estimated using Eq. (1) (Johnson and Elizondo 1979):

$$K = (M - E_{\text{resp}}) / (T_c - T_{sk}) \quad (1)$$

Statistical analysis

Data were analyzed using the statistical analysis system (SAS). All data were examined for normality of distribution (Proc Univariate Normal) and homogeneity of variance (Levene's test), and transformed to a log or square-root function where necessary to meet assumptions of analysis of variance (ANOVA). Data were then analyzed using Proc Mixed and two-way ANOVA with temperature and humidity as main factors and monkeys as a random factor. Comparison of individual treatment means was made by either a priori orthogonal contrasts or via the a posteriori Bonferroni test with adjusted probability levels to compensate for multiple comparisons. Where appropriate, relationships between parameters were analyzed for differences between humidity levels by analysis of covariance (ANCOVA). All data in Results are expressed as mean \pm SEM of original data. Differences with $p < 0.05$ were accepted as statistically significant.

Results

The female rhesus monkeys of this study maintained a relatively constant T_c over the range of ambient temperatures from 25–35 °C irrespective of ambient humidity (see Fig. 1A). Analysis of variance revealed a significant effect of ambient temperature ($F=12.46$, $df=32$, $p < 0.05$); the magnitude of the increase in T_c with increasing ambient temperature was related to the absolute humidity of the climatic chamber. At the highest humidity, T_c continued to rise during the experiment, yielding a significant increase in T_c under this condition between 35 and 40 °C; T_c measured during the same experimental period as in other treatments was significantly higher than at other ambient temperatures. In order to ensure the safety of the monkeys, experiments at 40 °C and 40 torr were discontinued if T_c rose above 40.5 °C. Thus, we cannot exclude the possibility that the monkeys might have achieved thermal balance at 40 torr at a slightly higher T_c with increasing heat loss via nonevaporative avenues.

T_{sk} also increased with ambient temperature ($F=102.73$, $df=32$, $p < 0.05$), but there were no significant effects of absolute humidity ($F=1.18$, $df=32$, $p=0.32$) on the magnitude of the increase (Fig. 1B). Linear regression analysis revealed a highly significant relationship ($r^2=0.88$, $p < 0.05$) between T_{sk} and the

temperature of the dry-bulb thermometer of the climatic chamber. Regression analysis of T_{sk} on the wet-bulb thermometer temperature, however, revealed that T_{sk}

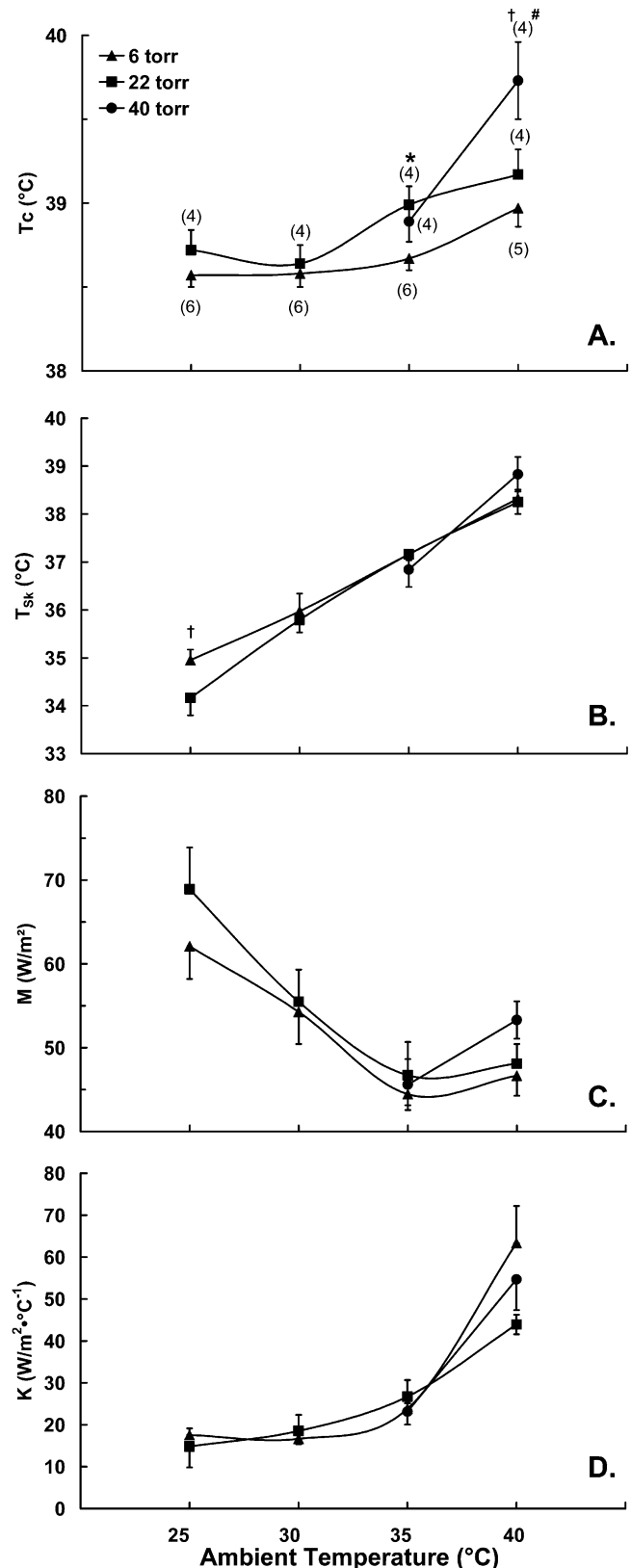


Fig. 1A Thermoregulatory parameters of rhesus monkeys as a function of ambient temperature. **A** Colonic temperature (T_c); **B** skin temperature (T_{sk}); **C** metabolic rate (M); **D** whole body conductance (K). The sample size (n) for each measurement is indicated in parentheses in **A**. Significant difference between values in humidity environments: asterisk (*) 6 vs. 22 torr; single dagger (†) 6 vs. 40 torr; hash (#) 22 vs. 40 torr. For clarity, significant differences between temperature values at any given absolute humidity are not designated

was independent of wet-bulb temperature, i.e., humidity had no direct effect on T_{sk} .

The relationship between M and ambient temperature is shown in Fig. 1C. M of the rhesus monkeys of this study presents the typical endothermic profile, in that M increases ($F=16.48$, $df=32$, $p<0.05$) at ambient temperatures below the animals' lower critical temperature to offset heat loss and begins to increase slightly above the upper critical temperature as the animals begin to store heat. Because the data were collected at 5 °C increments, we do not have the resolution necessary to establish definitively the limits of the thermoneutral zone as done previously (Johnson and Elizondo 1979). At ambient temperatures clearly below the thermoneutral zone, M changed with a slope of $-2.16 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$ at an ambient vapor pressure of 6 torr. At a higher vapor pressure (22 torr), the slope of the relationship between M and ambient temperature tended to increase to $-2.68 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$ below the lower critical temperature, although this rise did not achieve statistical significance. Likewise, at 40 °C, M tended to increase with humidity from $46.66 \pm 2.38 \text{ W m}^{-2}$ to 48.08 ± 2.34 and $53.3 \pm 2.22 \text{ W m}^{-2}$ at 6, 22 and 40 torr ambient vapor pressures, respectively. However, analysis of variance demonstrated that absolute humidity had no effect across all ambient temperatures ($F=1.43$, $df=32$, $p=0.25$).

Whole-body conductance (K) was significantly influenced by ambient temperature ($F=63.51$, $df=32$, $p<0.05$), increasing from minimal values of $14.8\text{--}17.6 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$ at 25 °C to $23.1\text{--}26.7 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$ at 35 °C and then significantly to $43.9\text{--}63.3 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$ at 40 °C (Fig. 1D). Humidity had no significant impact on K , however ($F=0.55$, $df=32$, $p=0.58$).

Total evaporative heat loss and the individual heat exchanges due to largely respiratory water loss (head chamber) and sweating from the remainder of the body are presented in Fig. 2. Upon entry to the chamber, we found relatively "dry" monkeys; the only wetness ever noted was on the forehead, and there was no evidence of sweat having run off onto the neck plate of the restraint chair. Total evaporative heat loss (E_{tot}) increased as ambient temperature increased ($F=13.83$, $df=31$, $p<0.05$), but increases were not dependent on humidity ($F=1.46$, $df=31$, $p=0.25$; Fig. 2A).

Evaporative heat loss measured from the head chamber (inclusive of respiratory evaporative water loss and any sweating from the head) was significantly affected by temperature ($F=21.72$, $df=32$, $p<0.05$; Fig. 2B) and humidity, as the 40-torr ($5.0 \pm 0.7 \text{ W m}^{-2}$) value was significantly less than the values for either 6 torr ($9.0 \pm 0.8 \text{ W m}^{-2}$) or 22 torr ($8.1 \pm 1.0 \text{ W m}^{-2}$) at 40 °C ($F=9.67$, $df=32$, $p<0.05$; Fig. 2B). Evaporative heat loss via sweating from the remainder of the body also increased with temperature ($F=12.67$, $df=31$, $p<0.05$; Fig. 2C). In this case, however, analysis of variance revealed no significant relationship between evaporative heat loss due to sweating and ambient humidity ($F=1.67$, $df=31$, $p=0.21$), even at the highest

ambient temperature (50.6 ± 12.1 , 56.4 ± 8.5 , and $39.9 \pm 4.7 \text{ W m}^{-2}$ for 6, 22 and 40 torr, respectively). Because the magnitude of evaporative heat loss measured from the head chamber was much less than that produced by sweating from the remainder of the body, there was no statistically significant effect of humidity on E_{tot} , despite its attenuation of evaporative heat loss from the head chamber (Fig. 2A).

Neither temperature ($F=2.66$, $df=32$, $p=0.06$) nor humidity ($F=0.34$, $df=32$, $p=0.72$) produced statistically significant alterations in HR (data not shown).

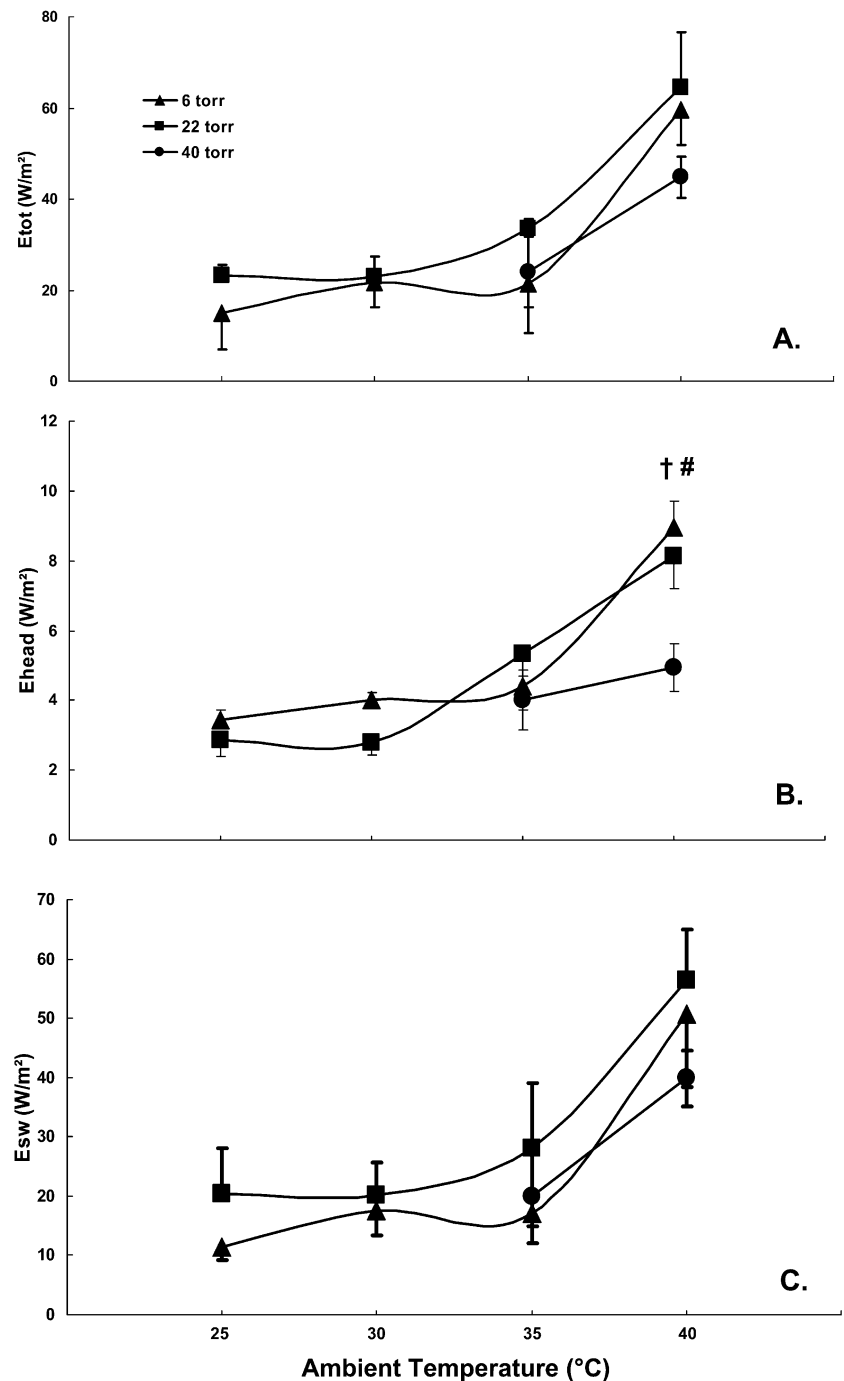
Discussion

Rhesus monkeys are capable of achieving thermal balance (i.e., regulating T_c within a narrow range) over a broad range of temperature and humidity conditions. However, thermal balance was achieved at higher core temperatures at ambient temperatures of 35 and 40 °C at both of the higher humidities. This is the most commonly reported effect of high humidity on thermoregulation in endotherms and confirms previous results of experiments using relative humidity rather than absolute humidity (Pandolf et al. 1974; Shvartz and Benor 1972).

At all humidities, total evaporative heat loss increased with increasing ambient temperature. The adequacy of evaporative heat loss for thermoregulation may be assessed by examining the ratio of evaporative heat loss to metabolic heat production. As seen in Fig. 3A, the ratio of E_{tot}/M increases with ambient temperature. At 25 and 30 °C, E_{tot}/M is less than 1, indicating the minimal importance of evaporative cooling at these temperatures. Instead, most heat loss at these temperatures occurs via non-evaporative avenues (i.e., conduction, convection, and radiation). At the highest ambient temperature, where non-evaporative heat exchange actually represented an avenue of heat gain to euthermic monkeys, an E_{tot}/M in excess of 1 indicates that there is sufficient evaporative cooling to balance the net gain of heat due to metabolism. Clearly, this occurs at absolute humidities of 6 and 22 torr. However, at an absolute humidity of 40 torr, E_{tot}/M at 40 °C is less than 1. Therefore, T_c rises under these conditions due to inadequate heat dissipation. Indeed, although absolute humidity did not significantly affect the total evaporative heat loss when graphed versus ambient temperature, examination of the relationship between T_c and E_{tot} (Fig. 3B) reveals that increases in ambient humidity progressively decrease the slope of the regression line describing this relationship. Therefore, at any given T_c , evaporative heat loss is diminished with increases in absolute humidity. As shown in Fig. 2, this decrease in evaporative heat loss was produced by attenuations of evaporative heat loss both from the head (approximately 4 W m^{-2}) and from the rest of the body (approximately $10\text{--}16 \text{ W m}^{-2}$).

Absolute humidity may influence evaporative heat loss in two ways. First, higher absolute humidities de-

Fig. 2 Total evaporative heat loss (A), head evaporative heat loss (B), and sweating evaporative heat loss (C) of rhesus monkeys as a function of ambient temperature. Sample sizes for each measurement are the same as those of Fig. 1. Significant differences between values in humidity environments: *single dagger* 6 vs. 40 torr; *hash* 22 vs. 40 torr. For clarity, significant differences between temperature values at any given absolute humidity are not designated



crease the physicochemical gradient along which water vapor moves from the skin. Second, a number of investigations have reported that sweat rate actually decreases as relative humidity increases in humans (Brebner and Kerslake 1964, 1968; Nadel et al. 1971; Nadel and Stolwijk 1973). Indeed, the rate of total evaporative heat loss is attenuated by increases in absolute humidity, as shown in Fig. 3B. The magnitude of this attenuation, however, was not as great as that observed in previous studies utilizing humans (Brebner and Kerslake 1964, 1968; Nadel et al. 1971; Nadel and

Stolwijk 1973). We speculate that this difference may be the result of species differences between humans and rhesus monkeys, in that the magnitude of sweating in these monkeys and, therefore, the potential for evaporative heat loss, is much less than that observed in humans (Gisolfi et al. 1982; Johnson and Elizondo 1979). In support of this contention, total evaporative heat loss in the patas monkey, a nonhuman primate that sweats more than the rhesus monkey (Gisolfi et al. 1982), approaches that of humans (Kolka and Elizondo 1983).

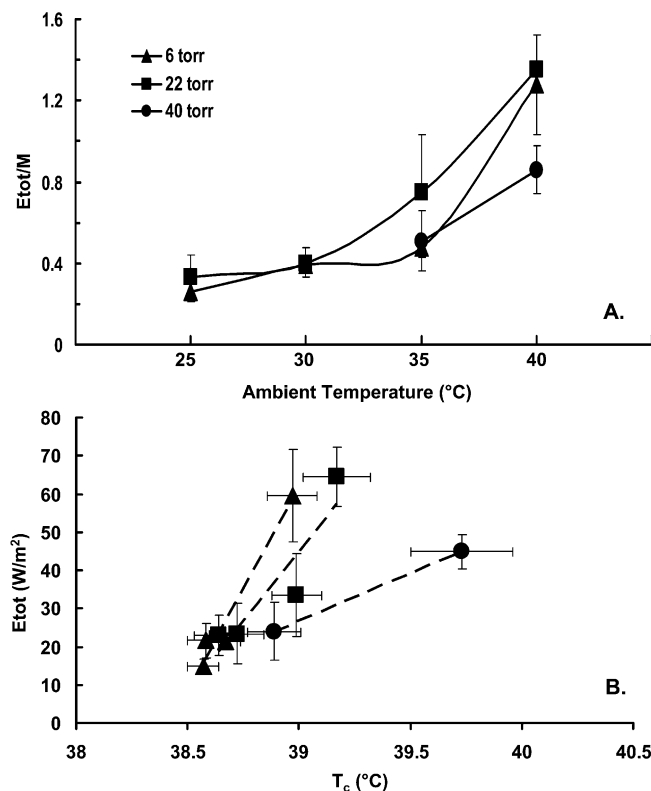


Fig. 3 **A** Ratio of total evaporative heat loss to metabolic heat production of rhesus monkeys as a function of ambient temperature. **B** Evaporative heat loss as a function of rectal temperature (T_c). Sample sizes for each measurement are the same as those of Fig. 1. For clarity, significant differences between temperature values at any given absolute humidity are not designated

The slope of the relationship between metabolic rate and ambient temperature, indicative of the rate of heat production necessary to offset heat loss for maintenance of T_c below the thermoneutral zone, did not vary significantly with humidity. In addition to suggesting a minimal, if any, shift in the lower critical temperature, this finding supports earlier studies of Iampietro and Buskirk (1960) who found little effect of humidity on thermoregulation by humans at temperatures below the thermoneutral zone. Thus, the primary effect of humidity on thermoregulation appears to occur at warmer ambient temperatures, particularly those above the upper critical temperature.

In conclusion, absolute humidity does not alter adjustments in metabolic rate within the temperature range of 25–40 °C in rhesus monkeys. Increases in absolute humidity do, however, produce decreases in evaporative heat loss, resulting in increases in core heating. These decreases in evaporative heat loss are accomplished via both humidity-dependent decreases in evaporative heat loss from the respiratory tract and evaporative heat loss due to sweating. These results using absolute humidity as the experimental perturbation therefore complement and extend previous investigations in which relative humidity has been used to

explore relationships between humidity and temperature regulation in primates, including man.

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